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THE SMALLEST NEW GUINEA ZYGOMATURINES-DERIVED DWARFS OR RELICT PLESIOMORPHS?

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ABSTRACT

Three Pleistocene species of zygomaturine diprotodontids are presently known from New Guinea. Two of these distinctive marsupials are much smaller than any of the late Tertiary zygomaturines that occurred in Australia, but are more similar in size to certain mid to late Miocene genera. Stirton *et al.* (1967). Flannery and Plane (1986) and Flannery (1988) have suggested that the late Tertiary New Guinea assemblages represent relict species with closest affinities to the mid to late Miocene faunas of Australia. A broad comparison of the morphology of late Pleistocene New Guinea zygomaturines indicates that they are derived species of the Australian Plio-Pleistocene *Zygomaturus* clade. As the relict fauna hypothesis appears to stem primarily from a "stage of evolution" interpretation of the New Guinea diprotodontids, this conclusion has significant implications for the palaeozoogeographic interpretation of New Guinea.

Keywords: Diprotodontidae, *Zygomaturus*, New Guinea, Tertiary biochronology, palaeozoogeography, marsupial systematics and morphology.

INTRODUCTION

Stirton (1967) and Plane (1967) originally observed that the New Guinea zygomaturine diprotodontids *Kolopsis rotundus* Plane and *Kolopsoides cultridens* Plane expressed closer affinities with the Australian Miocene species *Kolopsis torus* Woodburne than to any of the Plio-Pleistocene species of *Zygomaturus* Mcleay. At the time it was thought that the Awe Local Fauna (LF) was an early Pliocene-aged fauna. Moreover, it was generally held that the smaller diprotodontids were more primitive and therefore older than the larger species. In the next decade, Flannery and Plane (1986) described a small zygomaturine marsupial from the Pleistocene of New Guinea as *Hulitherium tomasettii* Flannery and Plane. They conclude that the monotypic *Hulitherium* also represents a relict species, reminiscent of certain Miocene genera known from the mainland of Australia. Shortly after their 1986 publication, another New Guinea Pleistocene zygomaturine was discovered in Irian Jaya. Though significantly smaller and apparently more specialized, this new diprotodontid shows some close resemblances to *Hulitherium*. This paper provides an alternative hypothesis of New Guinea zygomaturine phylogeny in which the available evidence is found to agree with revised radiometric dates and our current understanding of diprotodontid stage of evolution biochronology. I intend to establish the following points in the discussion: 1) that with the exception of *Kolopsoides cultridens*, all known Pleistocene New Guinea zygomaturines are members of the *Zygomaturus* clade; 2) the character states of all three New Guinea Pleistocene forms are derived relative to early to mid Pliocene *Zygomaturus* species known from mainland Australia; 3) there is sufficient biochronological and phylogenetic information to establish the most likely annectant for the New Guinea Pleistocene species; 4) consequently, it is possible to give an estimation of the time the genus *Zygomaturus* entered New Guinea; 5) that the size and morphology of the two smallest species is best explained as habitat related size-reduction or insular dwarfing; and finally 6) that the estimated time of arrival of zygomaturines in New Guinea does not support

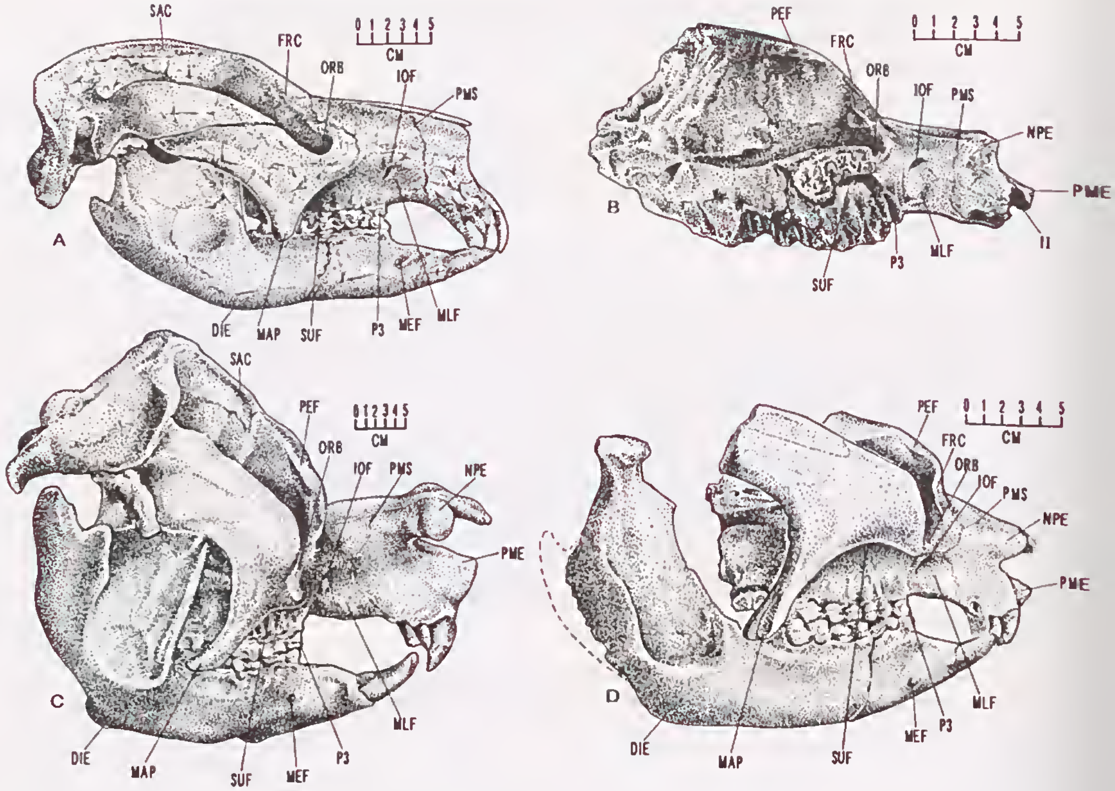

Fig. 1. Lateral aspects of representative zygomaturine crania, **A**, *Kolopsis torus*, Alcoota LF, Late Miocene, an advanced zygomaturine genus and likely structural precursor of *Zygomaturus*; **B**, *Hulitherium tomasettii*, Pureni LF, Late Pleistocene (drawn from photograph in Flannery and Plane 1986); **C**, *Zygomaturus trilobus*, Mowbray Swamp LF, Late Pleistocene (drawn from a cast prepared by Queen Victoria Museum, Launceston); **D**, N.G. *Gen. nov.* NTM P8660-1, P8660-2, P8668-3, Baliem LF, Late Pleistocene. Labels are defined in the key to anatomical abbreviations. Note deflected cranial bases, steep frontal profiles, deep suborbital fossae, short, deep zygomatic arches with and strap-like zygomatic processes (missing on B), low narial apertures and anteriorly situated orbits in B-D.

the hypothesis of an early Miocene faunal disjunction (Flannery 1988) from Australia.

Three Late Pleistocene New Guinea zygomaturines have each been assigned to different genera: *Hulitherium* (Flannery and Plane 1986), *Zygomaturus* (Hardjasasmita 1985); and a new genus, as yet undescribed (Flannery, pers. comm.) (Figs 1-2). I refer to T. Flannery's proposed new genus as "N.G. *Gen. nov.*" in order to avoid a nomen nudum. My observations on this new New Guinea species are based on another specimen (NTM P8660-1, P8660-2, P8660-3) that may differ somewhat from Flannery's proposed type, which I have not had the opportunity to examine first hand. However, the points I made at the CAVEPS symposium (Murray and Walker 1991) did not entail a formal description of the species, and it was only after I received a prepublication copy of Flannery's manuscript that I realized that there might be a potential problem.

At present, the majority of Australian Tertiary age estimations of Local Faunas are based on faunal correlations, primarily involving a succession of diprotodontid marsupials (Stirton *et al.* 1967, Archer *et al.* 1989). In light of recent revisions of the age of the Awe Fauna (Hoch and Holm 1986, Page and McDougal 1972), the systematic conclusions in Stirton *et al.* (1967) and Flannery and Plane (1986) imply that biostratigraphic age determinations for New Guinea are inherently unreliable. In re-examining some of the morphological evidence relating to the apparent discrepancy in stage of evolution correlations with radiometric age determinations for New Guinea, I found that a relatively minor re-interpretation of the data places the biochronological evidence in accordance with the radiometric dates.

The genus *Zygomaturus*, which first appeared in the late Miocene Sandringham Sands at Beaumaris, Victoria, had differentiated into three

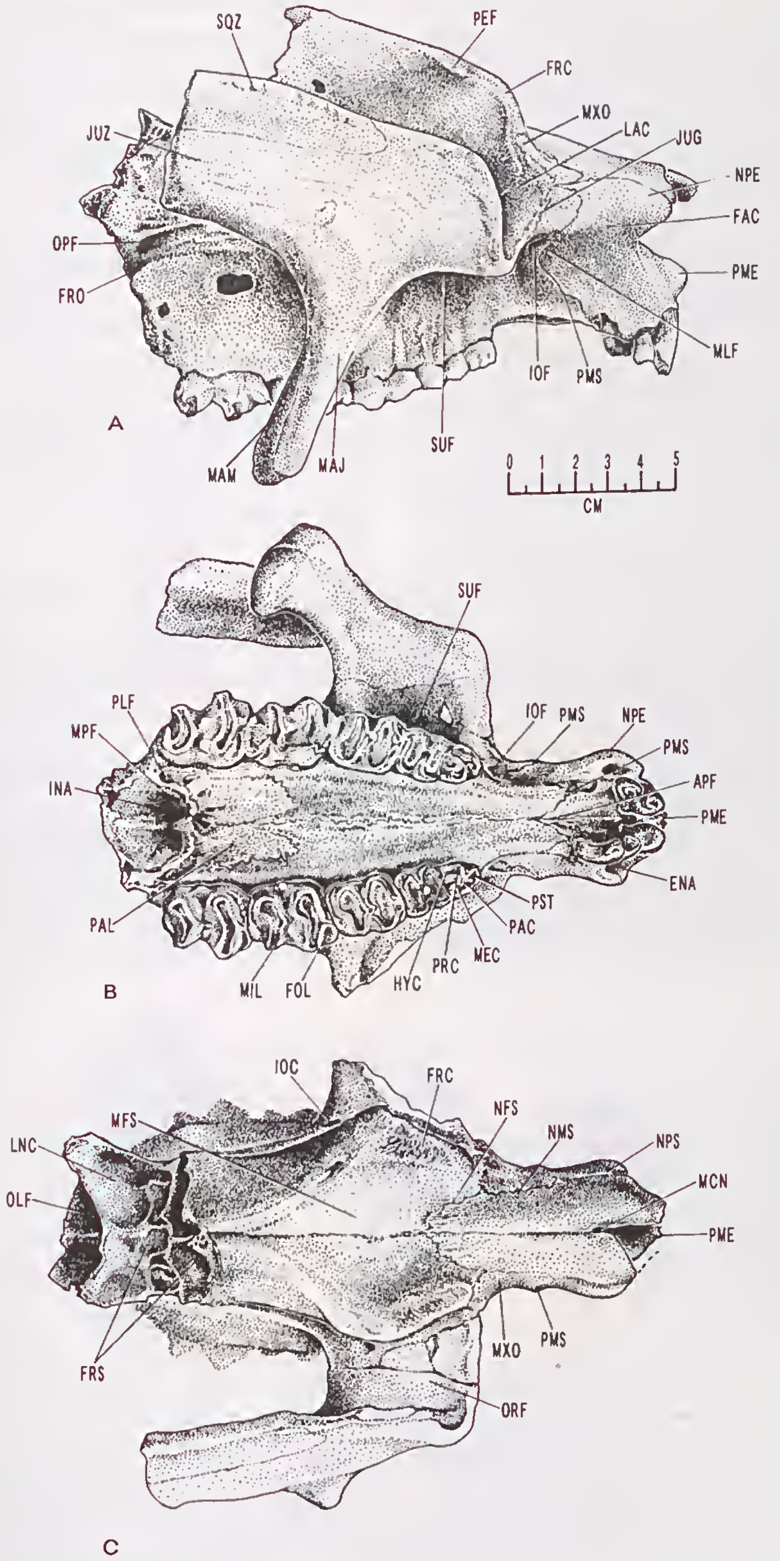

Fig. 2. Cranium of Baliem LF zygomaturine NTM P8660-1 (N.G. *Gen. nov.*), **A**, lateral aspect; **B**, ventral aspect; **C**, dorsal aspect; showing many similarities to the Australian Pleistocene species *Zygomaturus trilobus*. Labels are defined in key to abbreviations.

or perhaps four Australian species by the late Pleistocene (Stirton *et al.* 1967, Woodburne *et al.* 1985). There is no evidence for the existence of the genus before the late Miocene or early Pliocene (Woodburne *et al.* 1985).

The morphological succession toward *Zygomaturus* is based upon the addition of cusps and proportional changes in the permanent upper premolar crown; initially, the hypocone becomes a consistent feature in the mid Miocene genus *Neohelos* Stirton, followed by the division of the para-metacone into two distinct cusps in the late Miocene genus *Kolopsis* Woodburne (Stirton *et al.* (1967) (Fig. 3). Present in the mid to late Miocene were two basic zygomaturine clades: 1) plesiomorphous 3-and 4-cusped forms retaining an elongated, undifferentiated para-metaconal crest (*Neohelos*, *Plaisiodon* Woodburne, *Alkwertatherium* Murray) and 2) apomorphous 5-cusped forms with fully differentiated paracone and metacone (*Kolopsis* and *Zygomaturus*) (Murray 1990) (Figs 3-4).

A species of *Kolopsis* (Figs 1, 3-4) is the most likely structural precursor for *Zygomaturus* (Stirton *et al.* 1967, Woodburne *et al.* 1985, Murray 1990). Accordingly, the genus *Kolopsis* is the designated sister taxon of the genus *Zygomaturus*, constituting the plesiomorphic outgroup for phylogenetic analysis below the generic level. The genus *Kolopsis,* which apparently became extinct in Australia in the late Miocene, was thought to have persisted in New Guinea until the late Pliocene (Plane 1967, Woodburne *et al.* 1985). Evidence presented in this paper indicates that *Kolopsis rotundus* is a member of the *Zygomaturus* clade. The New Guinea zygomaturine genus *Kolopsoides* Plane, 1967, is considered here to represent a distinct derived lineage external to the *Kolopsis-Zygomaturus* ingroup.

ANATOMICAL ABBREVIATIONS

APF	Anterior palatal fenestra/incisive foramen
BC	Buccal cingulum
DIF	Digastric fossa
DIE	Digastric eminence
ENA	External nares
FAC	Facial crest
FOL	Forelink
FRC	Frontal crest
FRO	Foramen rotundum
HYC	Hypocone
I^n	Upper incisor
INA	Internal nares
IOF	Infraorbital foramen
JUG	Jugal
JUZ	Jugal portion of zygomatic arch
LAC	Lacrimal
LC	Lingual cingulum
LNC	Lamina of neurocranium
MAJ	Jugal portion of masseteric or zygomatic process
MAM	Maxillary portion of masseteric

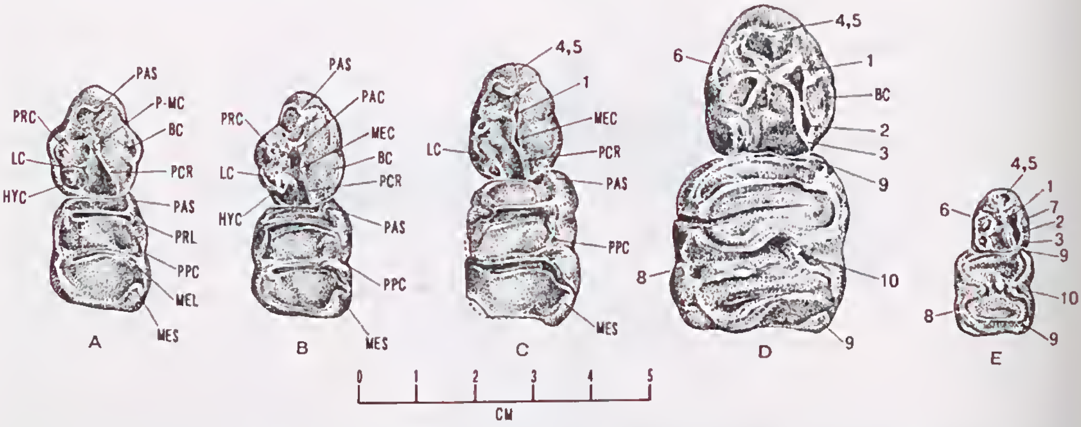

Fig. 3. Occlusal aspects of P^3 and M^2 of A, *Neohelos* sp. Bullock Creek LF, mid Miocene; **B**, *Kolopsis torus,* Alcoota LF, late Miocene; **C**, *Kolopsis sp. nov.* Ongeva LF, late Miocene; *Zygomaturus trilobus,* Victoria Cave LF, Late Pleistocene; **E**, N.G. *Gen. nov.* NTM P8660-1,, Baliem LF, Late Pleistocene. The morphological succession in dentition from *Neohelos* to *Zygomaturus* is gradual and continuous. *Zygomaturus* P^3 morphology is distingushed by a trend towards molarization, broadening of the crown and reduction of crown length relative to M^2. The four principle cusps become arranged in a square and the parastyle becomes more confluent with the outline of the crown. Large numerals refer to *Zygomaturus* synapomorphies given in Tables 1-2; labels on structures are defined in the key to abbreviations.

	or zygomatic process
MAP	Masseteric/zygomatic process
MCN	Median cleft between nasals
MEC	Metacone
MEL	Metaloph
MES	Metastyle
MFS	Median frontal sulcus
MIL	Midlink
MLF	Maxillo-labial fossa
MPF	Posteromedian palatine foramen
MX	Maxilla
MXO	Ossicle of maxilla
NPE	Naso-premaxillary eminence
NMS	Naso-maxillary suture
OLF	Internal cavity of olfactory bulb
OPF	Optic foramen
ORB/ORF	Orbit/orbital fossa
P^3	Permanent upper premolar
PAC	Paracone
PAL	Palatine
PCR	Postpara-metacrista
PEF	Postorbital eminence of frontal crest
PLF	Posterolateral palatine foramen
P-MC	Para-metacone
PME	Premaxillary eminence
PMS	Premaxillary-maxillary suture
PMX	Premaxilla
PPC	Postparacrista
PRC	Protocone
PRL	Protoloph
PST/PAS	Parastyle
PTF	Pterygoid fossa
SAC	Sagittal crest
SQZ	Squamosal process of zygomatic arch
SUF	Suborbital fossa

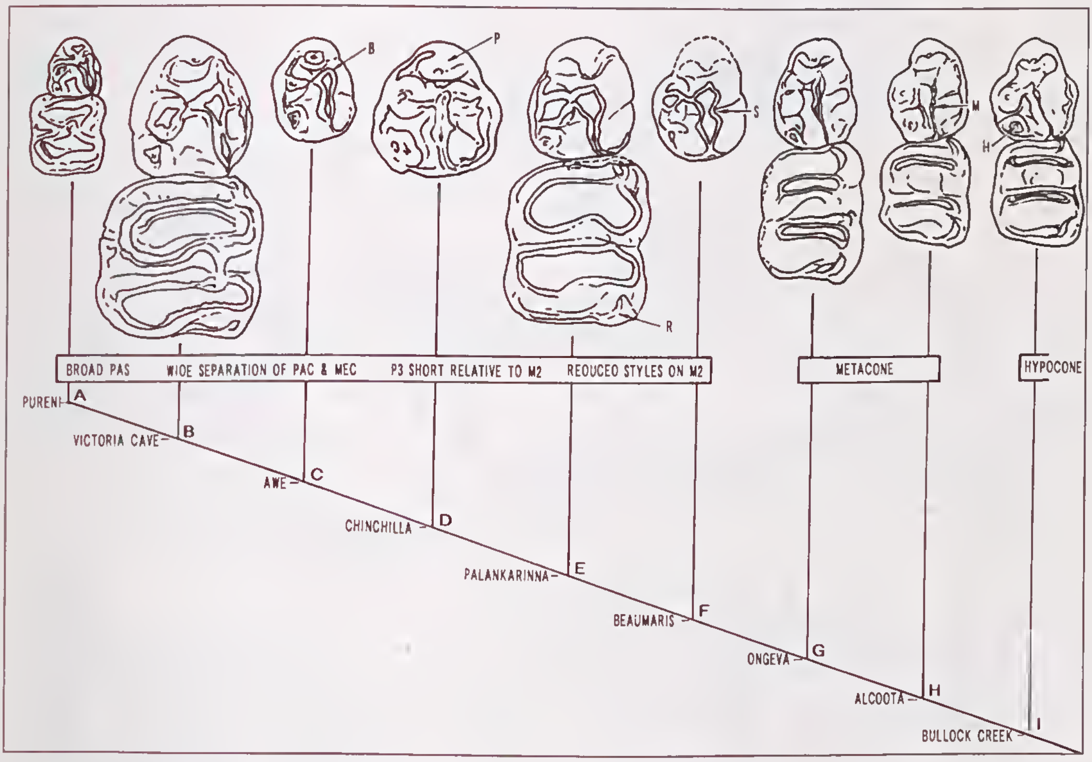

Fig. 4. Diagram depicting the broader cladistic units of the Zygomaturinae based on upper third premolar and second molar morphology; species are ordered stratigraphically according to the estimated age of respective local faunas; **A**, N.G. *Gen. nov.* Baliem LF, New Guinea, late Pleistocene; **B**, *Zygomaturus trilobus*, Victoria Cave LF, Naracoorte, S.A., late Pleistocene; **C**, *Kolopsis rotundus*, Awe LF, New Guinea, late Pliocene; **D**, Z. cf. *trilobus*, Chinchilla LF, QLD., late Pliocene; **E**, Z. *keanei*, Woodward Quarry, Palankarinna LF, S.A., late Pliocene; **F**, Z. *gilli*, Beaumaris LF, Vic., late Miocene-early Pliocene; **G**, *Kolopsis* sp., Ongeva LF, N.T., late Miocene; **H**, *Kolopsis torus* Alcoota LF, N.T., late Miocene; **I**, *Neohelos* sp., Bullock Creek LF, N.T., mid Miocene; drawn to scale. Abbreviations: H=addition of hypocone; M=differentiation of metacone from unitary para-metaconal cusp; S=increased separation of paracone and metacone accompanied by broadening of cusps; R=reduction of styles on M^2; P=closer approximation and broadening of parastyle; B=paracone and metacone situated closer to the buccal margin of the crown.

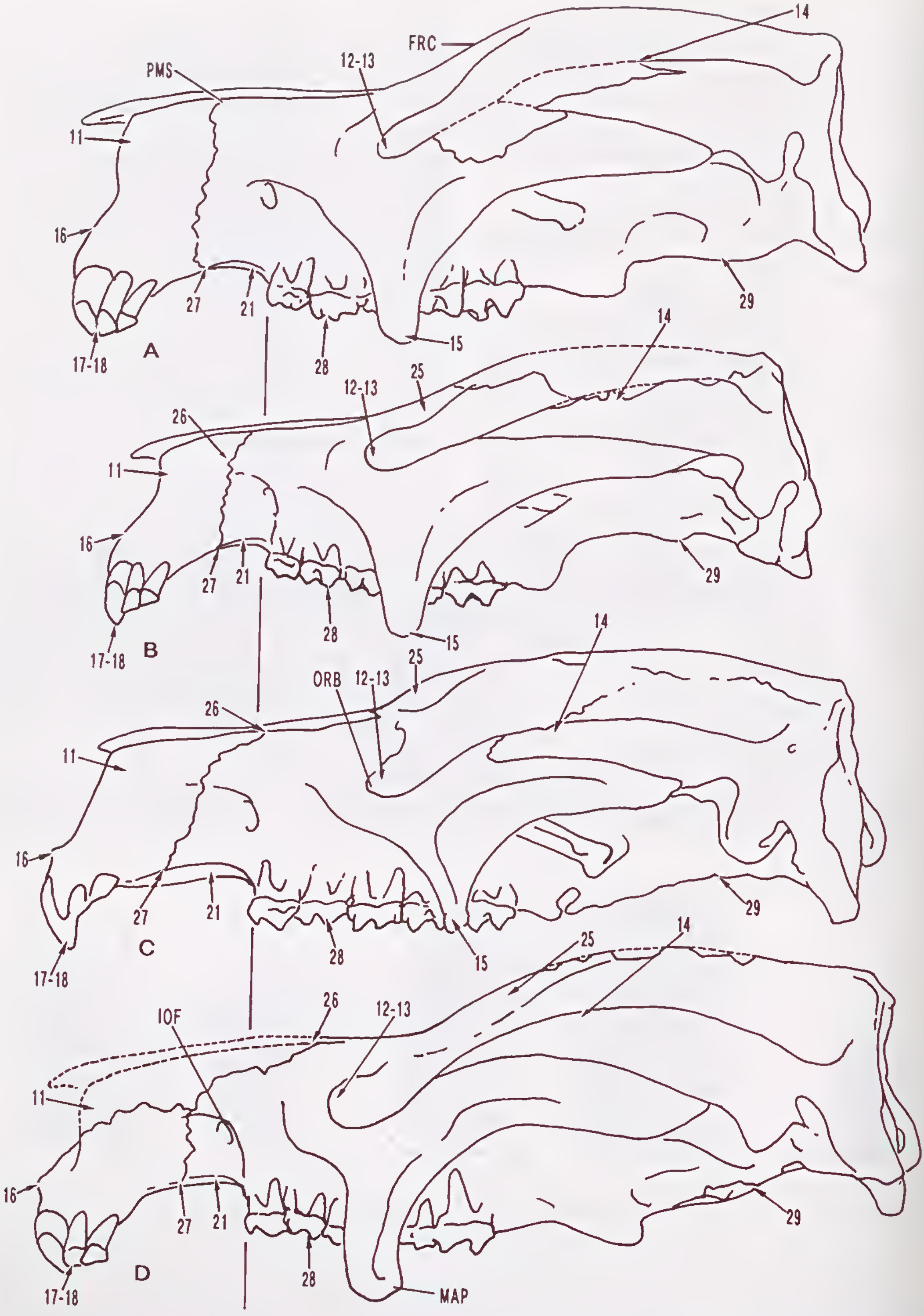

Fig. 5. Outlines of skulls of Australian Miocene zygomaturine genera representing plesiomorphic sister taxa of the genus *Zygomaturus*, scaled to equivalent cheek tooth row length for comparison; **A**, *Kolopsis torus*, Alcoota LF, late Miocene (X1/3); **B**, *K. torus*, Alcoota LF (showing typical size variation, possibly dimorphic), (X1/3); **C**, *Neohelos* sp., Bullock Creek LF, mid Miocene, (X1/3); **D**, *Plaisiodon centralis*, Alcoota LF (compare with type, Woodburne 1967: Fig. 32), late Miocene (X1/4). Small, narrow numerals depict symplesiomorphic states described in Table 1.

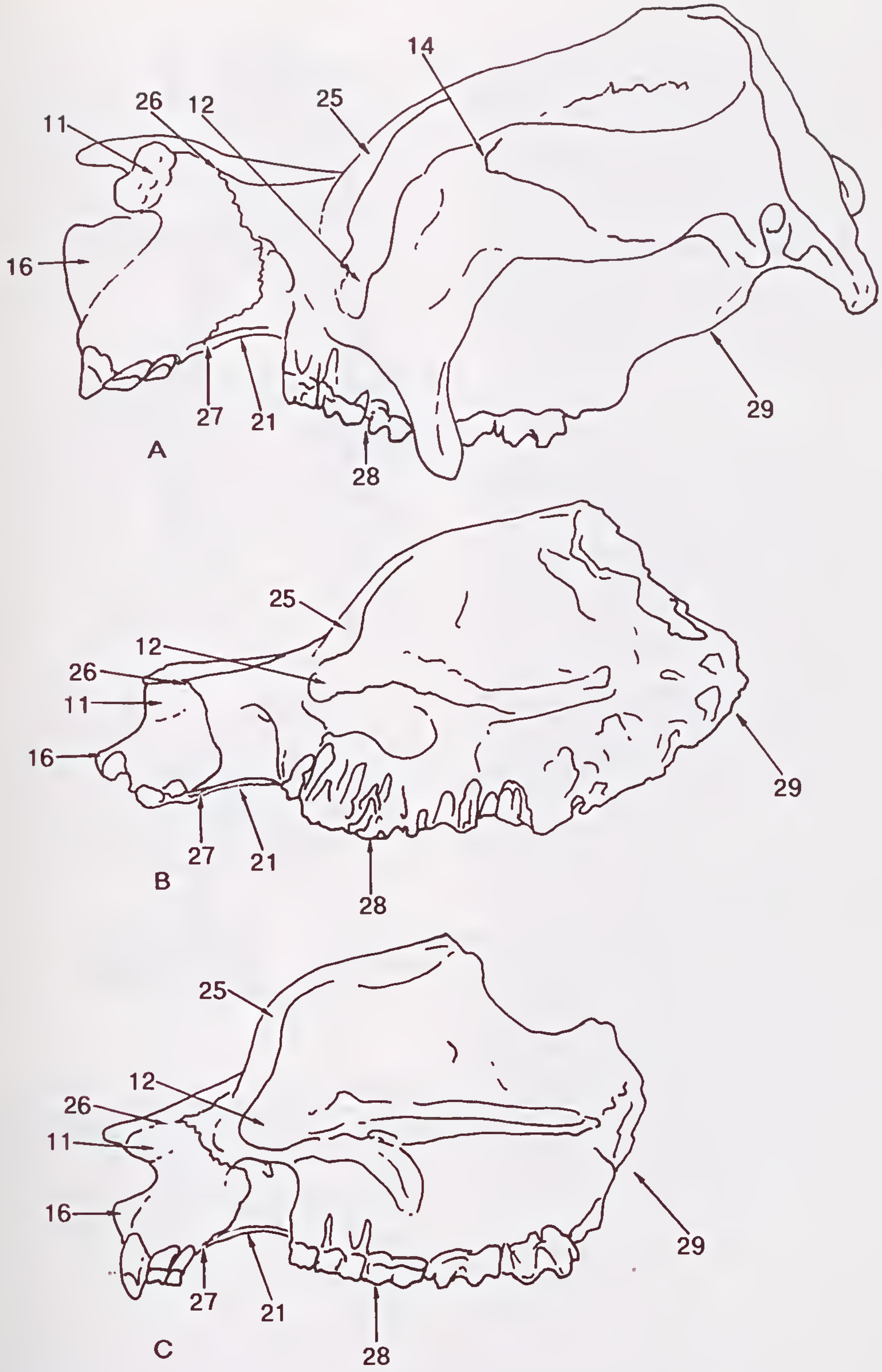

Fig. 6. Lateral aspects of crania of **A**, *Zygomaturus trilobus* (after Owen 1877); **B**, *Hulitherium tomasettii* (after Flannery and Plane 1986); **C**, N.G. *Gen. nov.* NTM P8660-1 showing *Zygomaturus* synapomorphies (large numerals, Tables 1-2); compare with previous figure (Fig. 5), the shape of the premaxillary-maxillary suture, position of orbit, profile of frontal, profile of narial aperture, proportions of cheek tooth row relative to rostrum.

MATERIALS

Northern Territory Museum (NTM) collection of Alcoota and Bullock Creek Local Fauna Diprotodontidae (*Kolopsis, Plaisiodon, Alkwertatherium, Pyramios* Woodburne, *Neohelos*); cranium and dentitions of *Z. trilobus*, Mcleay, Victoria Cave, South Australia; *Z. trilobus*, Mowbray Swamp, Tasmania (casts); cranium and two dentaries of *Zygomaturus* sp. nov., University of California, Santa Barbara, Department of Anthropology (original and NTM casts, P8660-1, P8660-2, P8660-3) Late Pleistocene, Baliem Valley, New Guinea.

RESULTS

Characteristics of Zygomaturus. *Kolopsis* is the plesiomorphic sister taxon of *Zygomaturus* on the basis of its synapomorphic possession of a divided para-metacone on the P^3 which, however, is plesiomorphic with regard to *Zygomaturus* in that the paracone and metacone are closer together, and the postmetacrista remains comparatively long. *Zygomaturus* apomorphies of the P^3 include closer approximation of the parastyle to the paracone and greater separation of the paracone from the metacone. The difference can be readily determined by noting the transverse alignment of the metacone with the hypocone in all known species of *Zygomaturus*, whereas in *Kolopsis* species the metacone is transversely aligned with the sulcus between the protocone and the hypocone (Figs 3-4).

Some other proportional differences are also apparent. For example, the para-metaconal crest in *Kolopsis* spp. is situated near the longitudinal midline of the crown whereas in *Zygomaturus* spp. it lies closer to the buccal margin (Fig. 3). In *Kolopsis* spp. the metastyle and parastyle of M^2 are large, flange-like crests. These structures are comparatively small in *Zygomaturus* spp. In *Zygomaturus* spp. the P^3 length is considerably less than the M^2 length. In *Kolopsis* spp. the M^2 is nearly equal in length or only slightly longer, than the P^3.

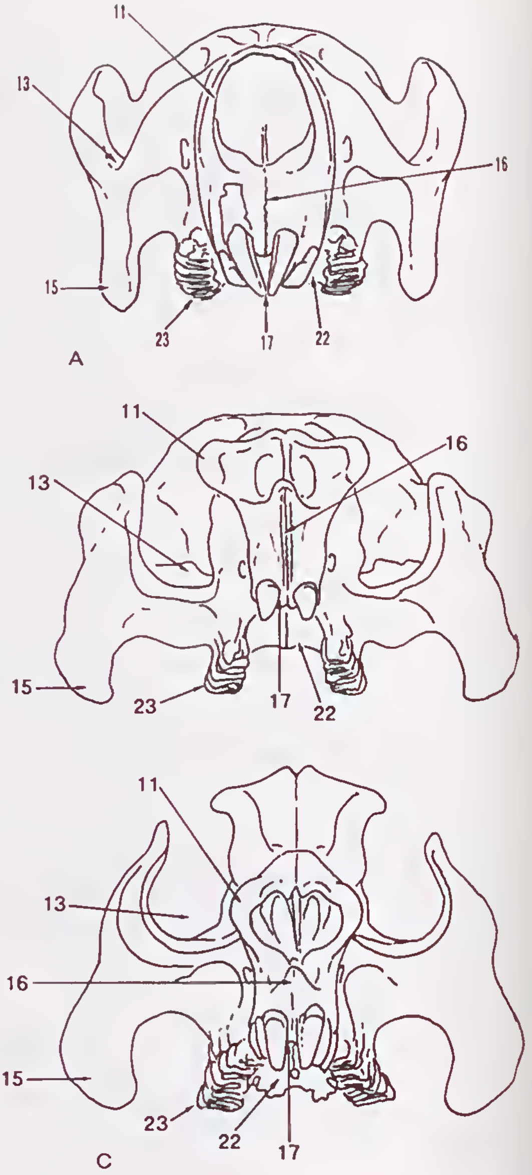

Fig. 7. Frontal aspects of crania of A, *Kolopsis torus*; B, *Zygomaturus trilobus* (after Owen 1877, note absence of sagittal crest in Owen's specimen in contrast to the well developed sagittal crest in the Tasmanian specimen): C, N.G. *Gen. nov.* NTM P8660-1 (tracing of a computer generated mirror-image restoration). Small numerals represent the plesiomorphic state of the morphocline, large numerals indicate *Zygomaturus* synapomorphics (Tables 1-2). Note the following strong contrasts in B and C with *Kolopsis torus* (A): transversely wide, low narial aperture with thickend dorsal margins compared to transversely narrow narial aperture with thin dorsal margins (11); frontally directed orbits compared to laterally directed orbits (13); laterally directed flange-like zygomatic processes compared to straight, conical processes (15); anterior convergence of cheek teeth (23).

Zygomaturus possesses many other striking apomorphic contrasts with *Kolopsis* (Figs 5-10, Tables 1-2). Among the more obvious characters are the markedly reduced incisive foramina, anteriorly situated orbital margins, deep, bowed zygomatic arches and long transversely flattened zygomatic processes, presence of a flange-

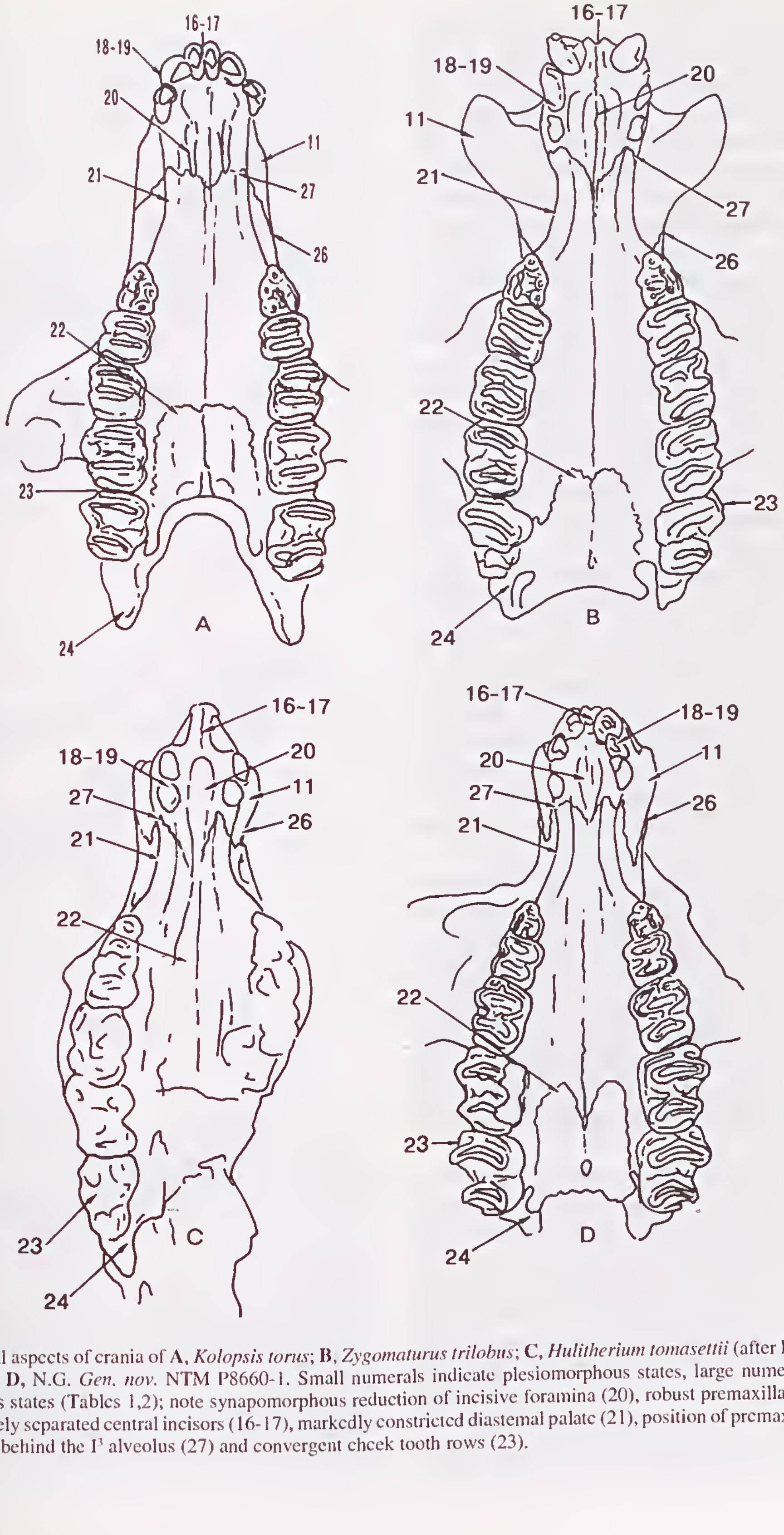

Fig. 8. Palatal aspects of crania of **A**, *Kolopsis torus*; **B**, *Zygomaturus trilobus*; **C**, *Hulitherium tomasettii* (after Flannery and plane 1986); **D**, N.G. *Gen. nov.* NTM P8660-1. Small numerals indicate plesiomorphous states, large numerals indicate apomorphous states (Tables 1,2); note synapomorphous reduction of incisive foramina (20), robust premaxillary eminence between widely separated central incisors (16-17), markedly constricted diastemal palate (21), position of premaxillary suture immediately behind the I^3 alveolus (27) and convergent cheek tooth rows (23).

like premaxillary crest between and above the central incisors, I^1 crowns widely separated and often divergent at the tips, chevron-shaped premaxillo-maxillary suture commencing immediately posterior to I^3, steep frontal profile and strongly deflected basicranial axis. These features are apparently interrelated in a functional complex that serves to place the bite force of the molars and the incisors closer to the fulcrum of the jaw.

Two primary modifications from the plesiomorphic state (*Kolopsis*) have occurred in *Zygomaturus*: 1) the ascending ramus of the dentary is reflected anteriorly, reducing the angle between the tips of the incisors and the digastric process and from the digastric process to the dentary condyle; 2) the width between the dentary condyles and the glenoid fossae is increased in relation to the distance from the condyles and glenoid fossae to the upper and lower incisor tips (Figs 11-12).

These modifications result in a relative lengthening of the lever arm for the m. masseter while reducing the length of the load arm of the dentary. As the ascending ramus has become more vertical, the maxillary alveolus has deepened in order to retain its occlusal relationship. On the inside of the jaw, the digastric fossa, due to its elevation, has become separated from the pterygoid fossa. In the more obtusely angled jaws of *Kolopsis* and *Neohelos*, the fossae are confluent (Fig. 9).

The position of the glenoid fossa is correspondingly elevated in relation to the occlusal line, resulting in a marked degree of upward flexion of the neurocranium. Because the linear dimension of the dorsal surface of the neurocranium is considerably shortened, the naso-frontal angle becomes less obtuse. The dorsiflexion of the neurocranium is also responsible for the anterodorsal rotatation of the jugal, which results in a distinctive lateral emargination of the orbit.

The splanchnocranium retains its upper incisive occlusal relationship with the increased recumbency of the lowers by a reduction of the length of the ventral premaxillary portion of the diastema. The complex shape of the premaxillo-maxillary suture in *Zygomaturus* is directly related to the overthrust of the fronto-naso-maxillary relationships dorsally, in reponse to neurocranial elevation and the ventral reduction of the length of the premaxilla.

The widening of the base of the triangle formed by the condyles and incisor tips reduces

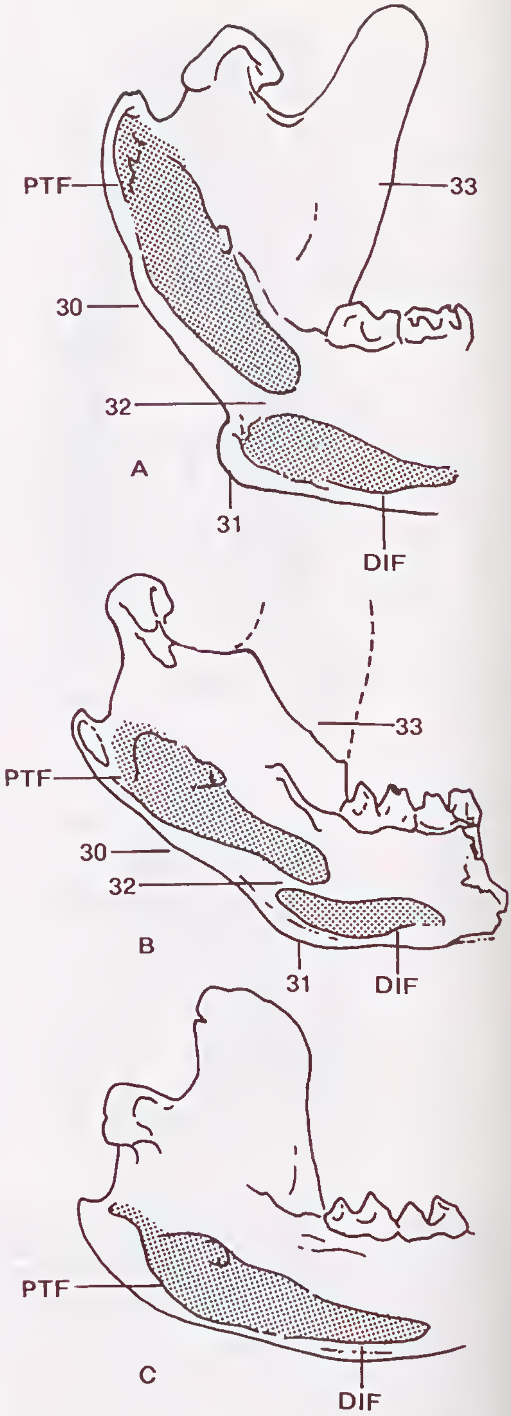

Fig. 9. Internal surfaces of dentary ascending rami **A**, *Z. trilobus*, Mowbray Swamp LF, Tasmania; **B**, N.G. *Gen. nov.* Baliem LF; **C**, *Kolopsis torus*, Alcoota LF. Note confluent digastric and pterygoid fossa in *K. torus*. Apomorphous states in A and B include erect or anteriorly inclined coronoid process (33); elevated angular process (30); separation of pterygoid and digastric fossae (32); posteriorly situated digastric eminence (31). Not to scale.

the amount of lateral excursion of the lower incisors in relation to the uppers but increases the vertical bite force exerted at the tips (Fig. 12). In *Kolopsis* the upper incisor arcade is broad, with small central incisors, whereas in *Zygomaturus* it is correspondingly narrow, with enlarged, tusk-like central incisors. Because relatively larger forces are exerted at the tips of the central incisors in *Zygomaturus* than in *Kolopsis*, the height of the narial aperture is reduced but widened, with concommitant bony thickening of the lateral and dorsal margins to resist bending moments on the rostrum.

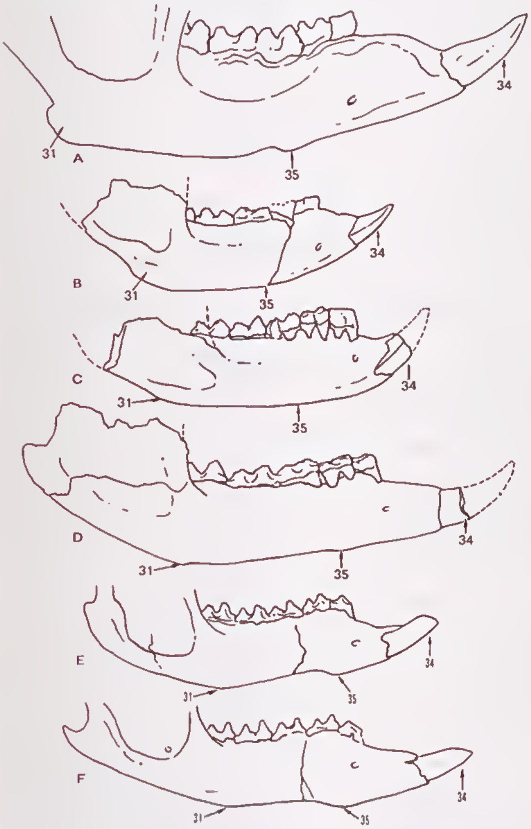

Fig. 10. Outlines of lateral aspect of horizontal rami of zygomaturines, drawn aproximately to scale; **A**, *Zygomaturus trilobus*, Mowbray Swamp, Tasmania; **B**, N.G. *Gen. nov.* (P8660-2, P8660-3) Baliem LF, New Guinea; **C**, *Kolopsis rotundus*, Awe LF, New Guinea; **D**, *Z. keanei*, Keane Quarry, Palnkarinna, S.A.; **E**, *Kolopsis torus*, Alcoota LF, N.T.; **F**, *Neohelos* sp., Bullock Creek LF, N.T. Small numerals indicate plesiomorphous character states, large numerals indicate apomorphous states (Table 1). Note pointed, recumbant lower incisors in A-C. The lower incisor of *Z. keanei* (D) is broken off. Other specimens are worn. However, they appear to have been as strongly curved as *Z. trilobus*. In P8660-2, the lower incisors are divergent as in *Z. trilobus*. Synapomorphous *Zygomaturus* features include pointed, divergent recumbant lower incisors (34); long symphysis (35); posteriorly situated digastric eminence (31).

In *Z. trilobus*, a large, thick bony flange of the premaxilla may also assist in the reduction of torsion on the snout, particularly in relation to asymmetrical biting on its divergent central incisor tips. However, the premaxillary flange also may have supported the labial retractor muscles of a prehensile upper lip. Many large, short-faced herbivores (e.g. elephants, rhinos) have evolved selective feeding mechanisms to compensate for the absence of a long, narrow snout.

The anterior end of the cheek tooth arcades are more convergent in *Zygomaturus* than in *Kolopsis* (Figs 7-8, 12). According to Greaves (1978), anterior convergence of the cheek dentition acts to increase the force at the anterior teeth by shortening the resistance lever arms. Moreover, in conjunction with the increased bite force along the posterior portion of the cheektooth row, the front-to-back gradient is greatly increased, with conspicuous enlargement of M^{4-5}; while the anterior end is correspondingly reduced in both length and width, especially P^3 and M^2. The cheektooth arcade is curved, retaining the same linear proportions as in *Kolopsis* but simultaneously increasing the occlusal surface area of the posterior half of the molar row. In lateral aspect, a slight curve of Spee is developed in response to the higher angle of occlusal moment.

I consider the inferred functional features of the skull outlined above to be co-dependant with the dental apomorphies that have long served to distinguish known *Zygomaturus* spp. from *Kolopsis* or *Plaisiodon* (Stirton *et al*. 1967), (Fig. 4, Tables 1-2). The upper third premolar of the genus *Zygomaturus* shows a clear trend towards molarization and antero-posterior compression of the anterior portion of the cheek tooth arcade, which is in agreement with Greave's (1978) functional interpretation of short-faced browsers. At the generic level, the unique features of the cheek teeth of *Zygomaturus* are integral components of its trophic specializations.

Because the characters used in this analysis are all considered to be part of a distinctive adaptive complex not manifestly present in the outgroup (*Kolopsis torus*), it follows that they collectively represent a synapomorphy for *Zygomaturus*. However, the states of various characters within the apomorphic complex may be indicative of the phylogenetic relationships of respective clade members. The horn-like nasal protuberances (naso-premaxillary eminences), greatly enlarged premaxillary flange (premaxil-

Table 1. Character state polarities of *Zygomaturus* determined by comparison of *Zygomaturus* species with *Kolopsis torus* outgroup.

		CHARACTER	APOMORPHIC	PLESIOMORPHIC
P^3	1	PAC & MEC	widely separated	close together
	2	para-metacristae	buccal	near midline
	3	postmetacrista	short, steep	long, inclined
	4	PAS to PAC gap	narrow	wide
	5	PAS width	broad	narrow
	6	occlusal shape	short, broad	long broad
	7	buccal cingulum	weak-absent	strong
M^2	8	occlusal shape	square, broad	trapezoidal
	9	styles	reduced	large
	10	mid-valley	narrow, occluded	wide, open labially
CRANIUM	11	narial aperture	low, broad, thick	high, narrow, thin
	12	orbit position	above P^3	above M^3
	13	orb. orientation	frontated	lateralized
	14	zygomatic arch	short, deep, bowed	long, straight
	15	zygom. process	long, transverse	short rounded
	16	pmx crest	present	absent
	17	upper I^1	I^1 large separated	I^1 small, convergent
	18	upper I^{2-3}	small	large
	19	incisor arcade	narrow, u-shaped	broad, c-shaped
	20	incisive foramen	small, vestigial	very large
	21	upper diastema	short, constricted	long, wide
	22	palate	deep, arched	shallow, flat
	23	cheek tooth row	convex, convergent	straight, parallel
	24	postalv. proc.	Short	long
	25	frontal crests	large, vertical	moderate, inlined
	26	sup. PMX-MX sut.	Anterior	posterior
	27	inf. PMX-MX sut.	Close to I^3	far from I^3
	28	occlusal plane	convex	straight
	29	cranial base	marked flexion	slight flexion
DENTARY	30	ascending ramus	elevated, upright	low, inclined
	31	digastric proc.	Strong, posterior	weak, anterior
	32	ramal fossae	separated	confluent
	33	coronoid process	projects anteriorly	inclined posteriorly
	34	lower incisor	recumbent, pointed	procumbent, blunt
	35	symphysis	long, deep	short, shallow

lary eminence), extremely large body size and the exaggerated frontal and orbital protuberances of *Zygomaturus trilobus* are autapomorphic features of that species. Conversely, the plesiomorphic retention of a well-developed buccal cingulum on the P^3 of *Z. trilobus* might indicate that it is a relatively early derivation of the clade. However, the expression of this relatively minor and variable character might also be interpreted as a size-related manifestation. In most other anatomical respects, *Z. trilobus* is fairly typical of the group.

I give the basic attributes of the skull and dentition of *Z. trilobus* greater taxonomic weight than its rather spectacular allometric distortions and autapomorhic protuberances. Consequently, my view of the phylogenetically significant synapomorphic features of the genus differs

Table 2. Distribution of character states in representative advanced zygomaturines; A=apomorphic state; P=plesiomorphic state; numerically designated characters defined in Table 1.

CHARACTER		*Kolopsis torus*	*Kolopsis* sp.	*Kolopsis rotundus*	*Zygomaturus gilli*	*Zygomaturus* cf. *trilobus*	*Zygomaturus trilobus*	*Zygomaturus keanei*	*Zygomaturus* sp. Lawson - Daily	*Hulitherium tomasettii*	N. G. *Gen. nov.*
P^3	1	A	A	-	A	A	A	A	A	P	P
	2	A	A	-	A	A	P	A	A	P	P
	3	A	A	-	A	A	A	A	A	P	P
	4	A	A	-	A	A	A	A	A	A	P
	5	A	A	-	A	A	A	P	A	A	P
	6	A	A	-	A	A	A	P	A	A	P
	7	A	A	-	A	P	P	A	A	A	P
M^2	8	A	A	A	A	A	-	-	-	P	P
	9	A	A	A	A	A	-	-	-	P	P
	10	A	A	P?	A	A	-	-	-	P	P
CRANIUM	11	A	A	-	-	A	-	-	-	-	P
	12	A	A	-	-	A	-	-	-	-	P
	13	A	-	-	-	A	-	-	-	-	P
	14	A	A	-	-	A	-	-	-	-	P
	15	A	-	-		A	-	-	?	P	P
	16	A	A	-	-	A	-	-	-	-	P
	17	A	A?	-	A?	A	-	-	A?	-	P
	18	A	A	-	A?	A	-	-	-	P?	P
	19	A	A	-	-	A	-	-	-	-	P
	20	A	A	-	-	A	-	-	-	-	P
	21	A	A	-	-	A		-	A?	-	P
	22	A	A	-	-	A	-	-	-	-	P
	23	A	A	-	-	A	-	-	-	-	P
	24	A	A	-	-	A	-	-	-	-	P
	25	A	A	-	-	A	-	-	-	-	P
	26	A	A	-	-	A	-	-	-	P	P
	27	A	A	-	-	A	-	-	-	P	P
	28	A	A?	-	-	A	-	-	A?	-	P
	29	A	A	-	-	A	-	-	-	-	P
DENTARY	30	A	-	-	-	A	-	-	A?	P	P
	31	A	-	-	-	A	-	-	A	P	P
	32	A	-	-	A?	A	-	-	A?	P	P
	33	A	-	-	-	A	-	-	A?	-	P
	34	A	-	-	A?	A	-	-	A	-	P
	35	A	-	-	A	A	-	-	A	-	P

somewhat from that of Flannery and Plane (1986). Polarities for the expression of characters in *Zygomaturus* were obtained by contrasting *Zygomaturus trilobus* with *Kolopsis torus* (Tables 1,2).

Small New Guinea species (*Hulitherium* and N.G.*Gen. nov.*). Outgroup comparison of the distribution and expression of characters among the species under consideration (Tables 1-2) indicates that *Hulitherium* and N.G. *Gen. nov.* are members of the *Zygomaturus* clade (Figs 4, 14). Both genera share virtually all uniquely *Zygomaturus* features such as arcuate premaxillary suture commencing immediately behind I^3, markedly reduced incisive foramina, precipitous frontal profile, infraorbital foramen situated close to anterior orbital margin, anterior orbital margin situated well forward over P^3, premaxillary crest developed between and above central incisors, thickened premaxillary margins of the external narial aperture and a strong meristic gradient between anterior and posterior cheek teeth. It follows that if *Hulitherium* and N.G. *Gen. nov.* are considered to be separate genera, then on cladistic grounds the differences among the other *Zygomaturus* species might also qualify them for separate genus rank distinctions.

Flannery and Plane (1986:66-67) state that *Hulitherium* "...possesses high vaulted frontals that are otherwise seen only in the species of *Plaisiodon* and *Zygomaturus*, and a reduced paracrista on M_2 and an anterodorsally directed maxillary-premaxillary suture, features otherwise seen only in species of *Zygomaturus*." A chip of enamel from the buccal side of P^3 shows that the paracone and metacone of *Hulitherium* are widely separated and that the postmetacrista is very short and steep. Moreover, Flannery and Plane (1986) noted that the P^3 of *Hulitherium* differs from *Z. gilli* "...in having the paracone and metacone closer at the buccal margin." The character distribution indicates that this is a derived feature of *Zygomaturus* species. In *Kolopsis* and primitive *Zygomaturus* species, the paracone and metacone slope lingually towards the midline of the crown. Consequently, *Hulitherium* expresses a more derived state of the *Zygomaturus* P^3 morphocline than does *Zygomaturus gilli* (Tables 1-2). Flannery and Plane (1986:74) place *Hulitherium* in its own genus as a possible sister taxon of *Zygomaturus* because: "In many features, *Hulitherium tomasettii* is more plesiomorphic than *Z. trilobus*...and because the postcranial morphology is markedly different from that of *Z. trilobus*, indicating an apparently long period of specialization...".

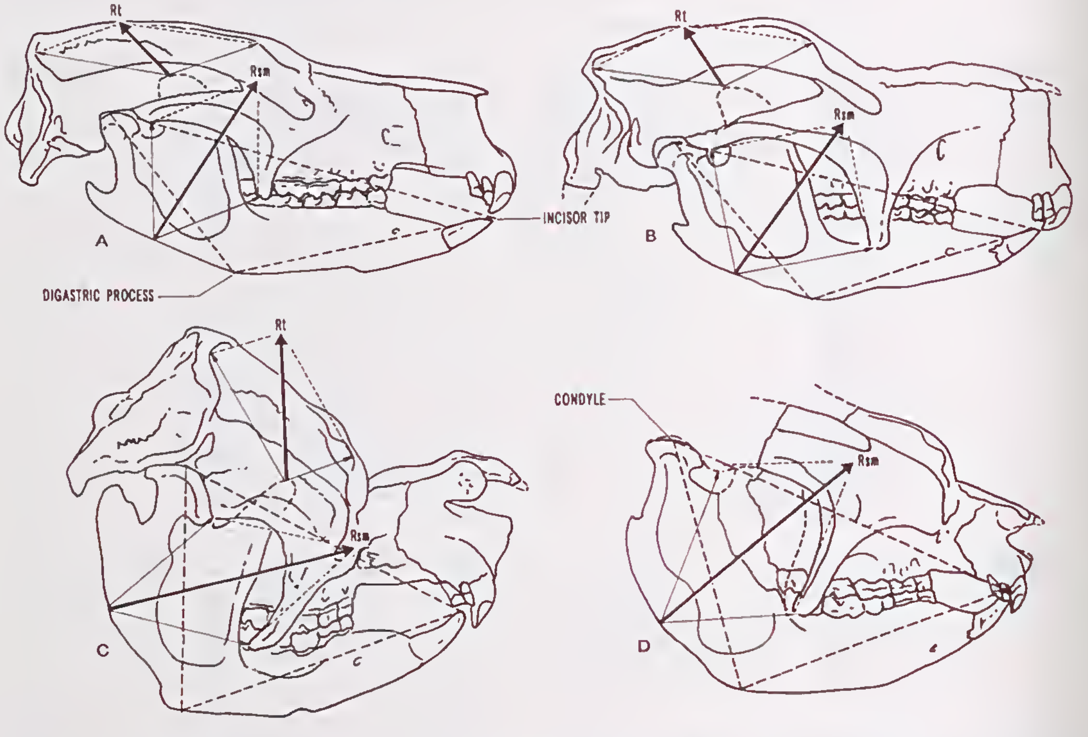

Fig. 11. Comparison of lateral aspect of skulls of plesiomorphic and derived zygomaturines; **A**, *Neohelos sp*; **B**, *Kolopsis torus*; **C**, *Zygomaturus trilobus*; **D**, N.G. *Gen. nov.* NTM P8660-1, P8668-2, P8668-3. Functional interpretation contrasts features of a distinctive trophic complex which members of the genus *Zygomaturus* (C-D) appear to share; A-D depict estimated resultant vectors for the m. temporalis (Rt) and m. superficial masseter (Rsm). Dashed triangles connecting condyle, incisor tip and centre of digastric process facilitate comparison. Though differing markedly in size, N.G. *Gen. nov.* (D) shows the same biomechanical modifications as *Z. trilobus* (C) in contrast to plesiomorphic zygomaturines (A-B). Measurements of individual components indicate that these modifications are predominantly isometries (rotations and translations); anisometries include shear in the rostrum, stretching in ventral border of the horizontal ramus and compression in the mid-face and zygomatic arches. Proportional sliding associated with scaling (enlargement-reduction) and allometry does not account for the modifications seen in C and D relative to A and B. However, allometry does account for differences between C and D, therefore small New Guinea zygomaturines show no specific anatomical relationships with small plesiomorphic Miocene zygomaturines.

Although they do not make the many plesiomorphic features of *Hulitherium* explicit, their statement conveys the idea that *Hulitherium* is a plesiomorphic sister taxon of *Zygomaturus* and that the affinities of *Hulitherium* are more with the Miocene genera *Kolopsis* and *Plaisiodon* than with other species of the genus *Zygomaturus* (i.e *Z. gilli* and *Z. keanei*). However, in the absence of comparable cranial material from the primitive *Zygomaturus* species *Z. gilli* and *Z. keanei* and in the absence of synapomorphic features of *Hulitherium* with *Kolopsis*, there appears to be no substance to their argument.

Based on NTM P8660-1, the recently proposed New Guinea genus (Flannery, pers. comm.), (N.G. *Gen. nov.*), (Figs 1-3) appears to be closely related to *Hulitherium* with respect to P^3 morphology (short steep postmetacrista), paracone and metacone lying close to buccal margin; strong front to back gradient in the cheek dentition, curved arcades with crowns large relative to the splanchnocranium, narrow, thin, high frontal crests and "dished out" frontal depression, deeply arched palate, low but distinct septal process of the premaxilla and small size compared to *Zygomaturus trilobus*. N.G. *Gen. nov.* differs from *Hulitherium* in being significantly smaller, in having a steeper, higher frontal profile, in possessing a more distinct nasomaxillary eminence and premaxillary interdiastemal crest. The orbital margins are more anteriorly situated, the rostrum is shorter and the molar crowns are more complex.

The shorter, relatively deeper rostrum of N.G. *Gen. nov.*, combined with incipient premaxillary-nasal eminences and a more prominent premaxillary crest, gives a closer resemblance to *Zygomaturus trilobus* than to *Hulitherium*. The similarities between N.G. *Gen. nov.* and *Z. trilobus* are more compelling in a restored comparison in which the large masseteric process and lateral orbital margin are shown (Figs 1-2). The zygomatic processes are unknown for *Hulitherium*. Also in common with *Z. trilobus*, the I^1 crowns of N.G. *Gen. nov.* (P8660-1) are slightly divergent in contrast to the markedly convergent crowns of *Kolopsis, Plaisiodon* and *Neohelos*. The state of this feature is not known for *Hulitherium*.

Although the dentition of N.G. *Gen. nov.* appears to be derived relative to *Hulitherium*, both genera are clearly synapomorphous with *Zygomaturus* and show strong polarity contrasts with *Kolopsis*. Due to the incompleteness of material available for an outgroup comparison at the species level, the question as to whether the more detailed similarities of N.G. *Gen. nov.* to *Zygomaturus trilobus* are genus rank parallels or species-rank synapomorphies cannot be resolved at present. At minimum, the phylogenetic evidence summarized in the figures and tables supports the inclusion of N.G. *Gen. nov.* and

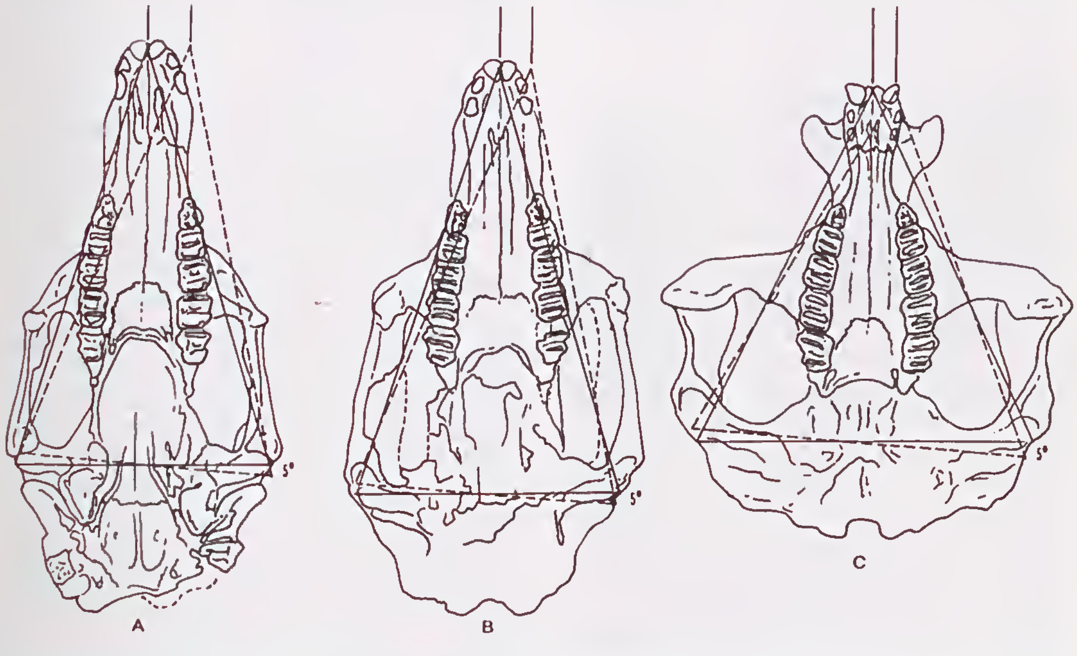

Fig. 12. Ventral aspects of **A**, *Neohelos* sp.; **B**, *Kolopsis torus* and **C**, *Zygomaturus trilobus* showing the extent of lateral excursion of the tip of the lower incisors in relation to a 5° displacement of the condyles.

Hulitherium within the *Zygomaturus* clade. If the more recent generic distinctions are to be retained, it may be useful to propose a new rank, Tribe Zygomaturini, to signify the clade affiliation and designate *Zygomaturus gilli* as a plesion or assign a new generic name to the species (Fig. 14).

Zygomaturus nimborensis **Hardjasasmita**. *Zygomaturus nimborensis* is a larger Pleistocene form about which very little is known. I have translated Hardjasasmita's (1985:1000) diagnosis from Bahasa Indonesia, which is here quoted in full: "Species diagnosis: A diprotodontid, Genus *Zygomaturus* that is much smaller than *Zygomaturus keanei*, but much larger than *Zygomaturus gilli*; mandible robust; ramus approximately horizontal; symphysis arises commencing at position of second molar; the hollow [internal contour] of the symphysis is diagonally slanted and bent in the letter U-shape. The height of the mandible is relatively great compared to molar height. Mental foramen diameter 0.5mm, situated under a line level with the molar crown. The valley between the anterior and posterior moiety (see figure 1 and figure 2) is curved like the letter U that is widest above. Type locality: near Nimboran, District Head, Genyem, near Sentani Jayapura, Irian Jaya. The exact location was not known [recorded]. Age: Estimated to be Pleistocene".

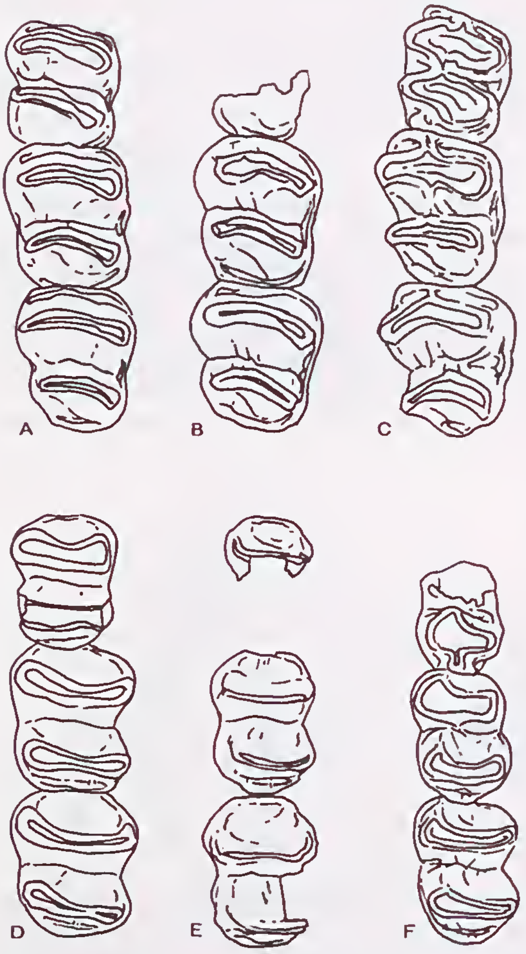

Fig. 13. Outlines of upper (A-C) and lower (D-E) cheek dentitions of **A**, Lawson-Daily Quarry *Zygomaturus*, Palankarinna LF (X2/3); **B**, *Kolopsis rotundus*, Awe LF (X1); **C**, N.G. *Gen. nov.*, NTM P8660-1, Baliem LF (X1); **D**, *K. rotundus*; **E**, *Hulitherium tomasettii*, Pureni LF (X9/10); **F**, N.G. *Gen. nov.* NTM P8660, (X9/10); scaled to length of M^5 for comparison.

The description, which merely elaborates on the fragmentary condition of the fossil, provides no additional information relevant to systematic assessment. My photocopy of the article contains no illustrations. The measurements given for the lower dentition of *Z. nimborensis* are of interest because of their approximate similarity in size to the upper molars of the Lake Palankarinna Lawson-Daily Quarry *Zygomaturus* (UCMP 70126), (Hardjasasmita 1985, Stirton 1967).

	M1	M2	M3	M4
Z. nimborensis (lowers)	—	29.8	32.8	36.2
Z. sp. UCMP 70126 (uppers)	—	30.0	34.3	33.7

The amount of variation between the upper and lower molars of the two species shown above is probably within the range of variation of a single species of the Zygomaturinae. However, Hardjasasmita's measurements also roughly correspond with the dimensions of *Nototherium watutense* Anderson, and should be considered particularly suspect with regard to the lack of reduction of M4, a feature also characteristic of *N. watutense*. I lack sufficient information to discuss this species any further.

Kolopsis rotundus. *Kolopsis rotundus* Plane, 1967 is a small Late Pliocene zygomaturine from the New Guinea Awe Fauna, Otibanda Formation (Figs 4, 10, 13). Its cheek dentition is slightly smaller than that of *Hulitherium* (Plane 1967, Flannery and Plane 1986). The specific diagnosis of *K. rotundus* (Plane 1967:111) includes a substantial inventory of *Zygomaturus* apomorphies: "Upper incisor not transversely compressed...; P^3 of similar size to that in *K. torus*; length 19.6... paracone and metacone 6.2 apart... [compared to 3.4 apart in a 21.0 long *K. torus* P^3] separated by wide lingual and labial

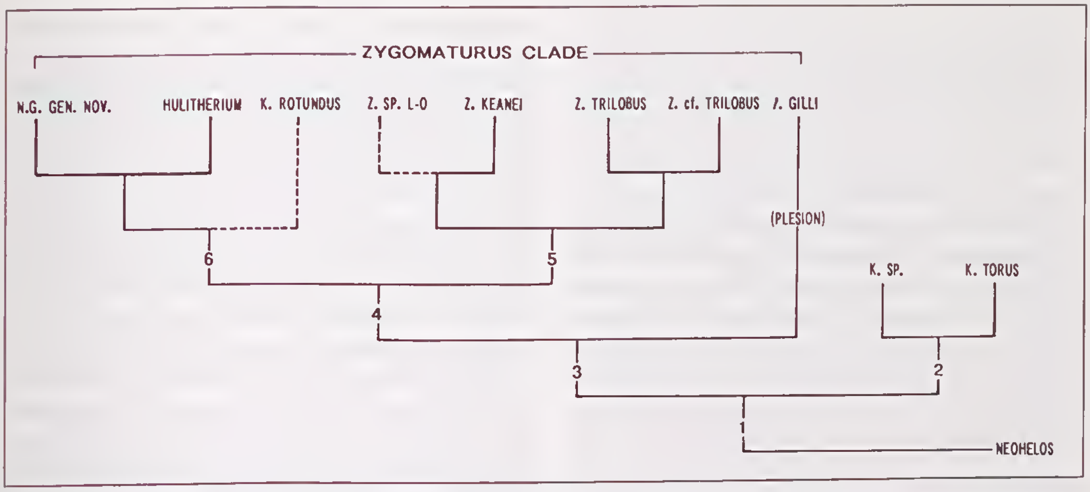

Fig. 14. Cladistic hypothesis of speciation in some representative Zygomaturini based on P^3 and M^2; N.G. GEN. NOV.=NTM P8660; Z. SP. L-D=Lawson Daily *Zygomaturus* sp.; Z. cf. TRILOBUS=Chinchilla *Zygomaturus* sp. (Archer and Bartholomai 1978); Apomorphies designated by numerals: 1, P^3 with 5 cusps; 2, incipient division of paracone and metacone on P^3, enlarged parastyles and metastyles on M^2; 3, P^3 paracone and metacone widely separated and enlarged, reduced parastyle and metastyle on M^2; 4, P^3 broad, short, reduced relative to M^2; 5, Wide labial sulcus with mesostyle and strong buccal cingulum on P^3; 6, P^3 paracone and metacone situated close to buccal margin, very reduced postmetacrista, narrow buccal sulcus and weak or absent mesostyle and buccal cingulum. Broken lines indicate possible closer connection between *K. rotundus* and Lawson-Daily *Zygomaturus* sp.

grooves; crest from metacone to posterior end of tooth short and steeply inclined...paracone and metacone more rotund than in *K. torus*; parastyle separated from paracone by much narrower transverse cleft than in *K. torus*...". The upper molars are larger relative to P^3 than in *K. torus*; the dentary is more robust; the digastric eminence and fossa are stronger. The lower incisor of *K. rotundus* is strongly curved, recumbant and pointed, unlike that of *K. torus* (straight, procumbent and blunt).

Plane (1976) does not elaborate on his reasons for excluding *Kolopsis rotundus* from the genus *Zygomaturus*. The specific contraindications are spelled out subsequently in Stirton *et al* (1967:156): the P^3 of "...the New Guinea species is more primitive than *Z. gilli* from Sandringham Sands... [in that the] posterolingual base of the protocone in *K. rotundus* not expanded to contact the anterolateral base of the metacone as in *Z. gilli*, small depression between protocone and paracone not developed in *K. rotundus*, shallower labial groove between paracone and metacone than in *Z. gilli*".

Such characters, particularly the small basin between the protocone and paracone, are not always present in *Zygomaturus trilobus*. I give more weight to the wide separation and robustness of the paracone and metacone, the short, steep para-metacrista, and broad, closely approximated parastyle of *K. rotundus* than to the apparently variable contraindicating features.

My interpretation of the character states for the genus *Zygomaturus* suggests that *K. rotundus* is a relatively derived species in having the P^3 paracone and metacone very widely separated and situated close to the buccal margin of the crown, also in possessing recumbent, pointed lower incisors and in several features of the dentary including a posteriorly situated digastric eminence and a conspicuously elevated ascending ramus (Tables 1-2, Figs. 4, 10, 13,).

Lawson-Daily Quarry *Zygomaturus*. Stirton (1967) reported on a *Zygomaturus* species recovered from the Lawson-Daily Quarry at Lake Palankarinna, South Australia, which he describes as being intermediate in size between *Z. keanei* Stirton and *Z. gilli* Stirton. Remarking on the upper molars of the specimen, he states: "the lophs are much as they are in *Z. keanei*, but even more like those in *Kolopsis rotundus* Plane, 1967 from New Guinea..." (Stirton 1967:145). They are indeed very similar (Fig. 13), *K. rotundus* differing only slightly in size and in having slightly more development of the lingual cingulum, anterior cingulum, crista obliqua and a relatively wider metaloph on M^5. The close similarities between *Kolopsis rotundus* Plane, 1967, and the Lawson-Daily *Zygomaturus* sp.

would indicate that both species represent the same genus and that they possess similarly derived character states.

Having remarked on the Lawson-Daily *Zygomaturus's* greater similarity to *Kolopsis rotundus* than to *Zygomaturus keanei*, it is unclear why Stirton (1967) did not propose placing them in the same genus. Presumably the decision to keep them separate was influenced by the apparent early Pliocene age of *Kolopsis rotundus* in the Awe Fauna, that was believed at the time to date between 7.6 and 5.7 million years BP (Everenden *et al.* 1964). That age determination has subsequently been adjusted upwards to between 2.5 and 3.5 million years BP (late Pliocene) (Page and McDougal 1972, Hoch and Holm 1986).

The revised K/Ar dates place *K. rotundus* in a biochronological context more compatible with the Lawson-Daily *Zygomaturus*. Simultaneously, the much younger revised age serves only to magnify the biochronological anomaly created by the apparent persistence in the late Pliocene of a *Kolopsis* species. Thus, the data support an alternative hypothesis suggesting that the earliest New Guinea Zygomaturini exhibit a stage of evolution comparable to that of a late Pliocene species of *Zygomaturus* from the southern portion of continental Australia.

DISCUSSION

If my hypothesis regarding the cladistic relationship of these zygomaturines is correct, the question of the origin and earliest time of arrival of *Zygomaturus* in New Guinea is virtually answered (Fig. 15). The Palankarinna LF is considered to be Kalimnan Stage equivalent. Thus, the Lawson-Daily *Zygomaturus* sp. is a late Pliocene form. The earliest known New Guinea zygomaturine, the Awe LF *Kolopsis rotundus*, is also a late Pliocene form. Evidence of a close relationship between *Hulitherium*, N.G. *Gen. nov.* and *K. rotundus* would result in a parsimonious explanation of the subsequent zygomaturine radiation in New Guinea.

Although the upper dentition of *Hulitherium* is poorly represented, the lower molars compare reasonably well with *K. rotundus*, differing primarily in size and in being slightly narrower relative to their length (Fig. 13). Flannery and Plane's (1986) description of the lower premolar fragment and molars of *Hulitherium* indicate a number of proportional and detailed structural similarities to *K. rotundus*, including crown and lophid shape, weak paracristid development, weak anterior cingulum, strong, rounded, centrally raised postcingulid, especially on M_{3-4} and faint cristid obliqua development. The fragment of *Hulitherium* P^3 indicates that it was similar to that of *K. rotundus* and N.G. *Gen. nov.* in having a widely separated paracone and metacone and a steep-sided, nearly vertical para-metaconal crest. There appear to be no features of the lower dentition of *Hulitherium* that could not have been derived from *K. rotundus*.

The dentition of N.G. *Gen. nov.* is elaborated in comparison to *K. rotundus* and *Hulitherium*. The molars are higher crowned, with thicker enamel, more prominent development of crests and cingulae and display a more marked front to back size gradient. The structure of the cheek dentition is basically similar sompared to *K. rotundus* in the uppers and compared to *Hulitherium* in the lowers (Fig. 13). The primary difference is in the development of distinct mid and hind links, which could have been derived from homologous, though much weaker structures present in *K. rotundus* and possibly *Hulitherium*, based on the analogous condition of its lowers. It is reasonable to suggest that a species with a lower molar morphology similar to *Hulitherium* or *K. rotundus* could have given rise to that of N.G. *Gen. nov.* (Figs. 13-15).

Arrival of *Zygomaturus* in New Guinea. The stage of evolution similarities between *K. rotundus* and the Lawson-Daily *Zygomaturus* would indicate that the genus *Zygomaturus* entered New Guinea no earlier than mid Pliocene. There is no evidence to support an earlier isolation of members of this or any other generic clade of the Diprotodontidae (Fig. 15). The Awe diprotodontine *Nototherium watutense* Plane, 1967, is also a derived species with closer affinity to the Pleistocene *Nototherium inerme* than to the late Miocene *Pyramios alcootense* (Stirton *et al.* 1967). *Kolopsoides cultridens* appears to represent an independent zygomaturine lineage, with no close affinities to *Kolopsis* or *Zygomaturus*.

I previously suggested (Murray 1990) that *Kolopsoides* may represent a parallel *Zygomaturus*-like development from a *Plaisiodon*-like ancestor. If this hypothesis is correct, *Kolopsoides* represents a stage of evolution structural equivalent to *Zygomaturus*. Because the mid to late Pliocene is poorly represented in northern Australia, no *Kolopsoides* annectants have been found. However, I speculate that these may eventually turn up on the mainland, possibly among the Riversleigh "System C" diprotodontids (Archer *et al.* 1989).

The character states of both *Hulitherium* and N.G. *Gen. nov.* suggest that they arose from a relatively derived species of the genus *Zygomaturus*. By analogy with certain other fossil taxa that make their appearance in the late Pliocene, I speculate that 3.5 million years could have been sufficient time for the development of their respective specializations, commencing with a form similar to *K. rotundus*.

Insular dwarfing or small plesiomorphs? The evidence does not support the hypothesis that *Hulitherium* and N.G. *Gen. nov.* represent relict small-sized plesiomorphic zygomaturines closely related to those from the Australian Miocene. The relatively small size of these two Pleistocene species might therefore be due to the phenomenon of insular dwarfing. Examples of very rapid and quite drastic body size reduction in mammoths are recorded in the late Pleistocene of North America and the Mediterranean in terms of thousands of years.

The most telling attribute of the small New Guinea Pleistocene zygomaturines is the conspicuous proportional differential between the cheek dentition and the facial skeleton. The basic configuration seen in *Zygomaturus trilobus* appears to be exaggerated in that the cheek dentition and the adductor muscle armatures are enlarged relative to the facial skeleton. This positive allometry of the trophic complex may indicate that the New Guinea zygomaturines are scaled down from a considerably larger species of *Zygomaturus*. The cheek dentitions of Miocene zygomaturine species are relatively small in proportion to their facial skeletons.

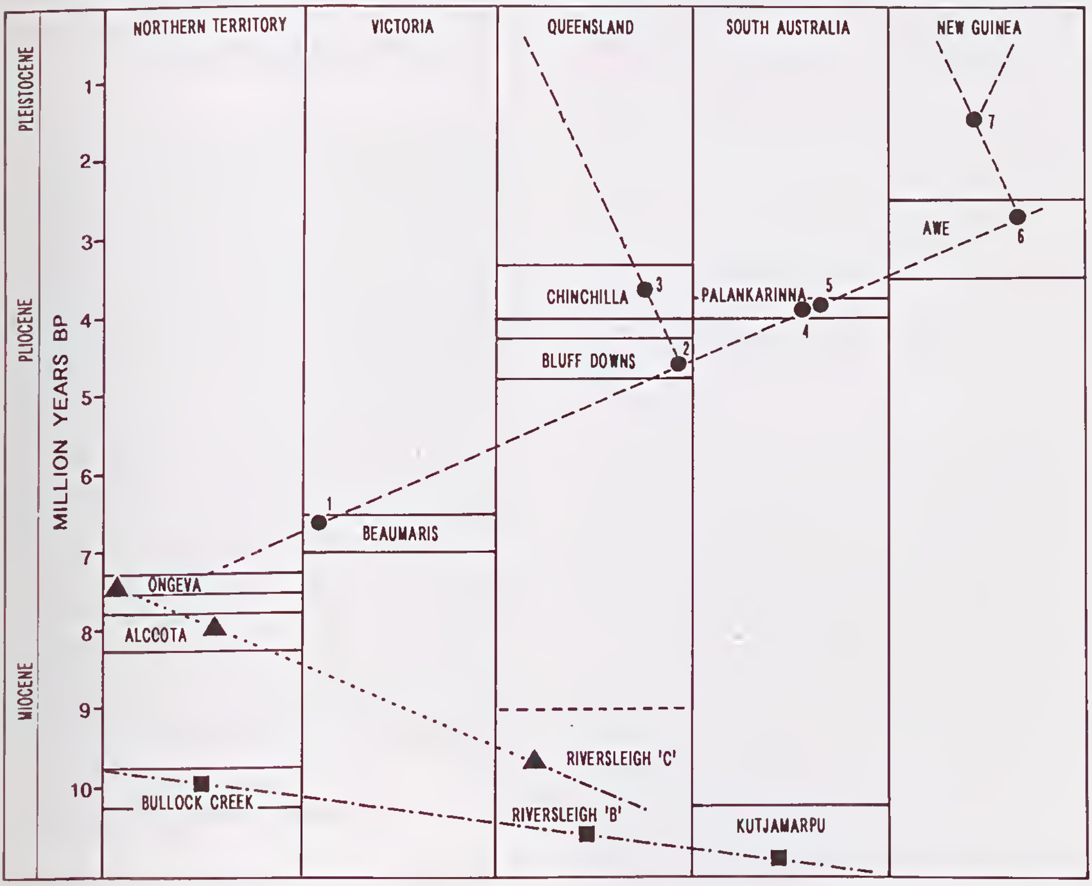

Fig. 15. Stratiphenetic diagram depicting a hypothesis of phyletic branching of zygomaturine annectants in relation to chronology; Dots=*Zygomaturus* clade; squares=*Neohelos* clade, triangles=*Kolopsis* clade; broken lines depict phyletic lineages connecting Local Fauna species as they occur in stratigraphic superposition; numerals designate *Zygomaturus* species: 1, *Z. gilli*; 2, *Z. sp*; 3, *Z.* cf. *trilobus*; 4, *Z. keanei*; 5, Lawson-Daily Quarry *Zygomaturus*; 6, *Kolopsis rotundus*; 7, small Pleistocene New Guinea *Zygomaturus* spp.; *Z. nimborensis* is not included as there are no specific morphological details upon which to base its position. Chronology is based on Woodburne *et al.* (1985).

It is unlikely that a simple size reduction in *Kolopsis torus* would result in a form similar to that of either *Hulitherium* or N.G. *Gen. nov.* and it is plainly evident that the only other explanation that would allow for the retention of a relict Miocene *Zygomaturus*-like form in New Guinea is to unparsimoniously postulate a highly detailed structural convergence with *Zygomaturus trilobus*.

The other Awe diprotodontids (*Nototherium watutense* and *Kolopsoides cultridens*), though apparently highly derived, are also much smaller than their closest late Miocene and Plio-Pleistocene relatives in Australia. It seems unlikely that all of these species are expressing independant parallel specializations in response to different selective pressures. A more parsimonious explanation for the phenomenon is insular dwarfing.

Implications for New Guinea palaeozoogeography. It now seems evident that an apparently minor systematic oversight has resulted in well over two decades of misguided theorizing about New Guinea zoogeography and an apparently anomalous zygomaturine biochronology (Stirton *et al.* 1967, Flannery 1988). Two misconceptions conspired to produce the notion that the New Guinea diprotodontid fauna represented a relict of Miocene Australia. By far the most influential factor was the initially incorrect radiometric age of the Otibanda Formation published by Everenden *et al.* (1964).

An age of 7.6-5.7 million years makes it seem just possible that the smaller mid to late Miocene diprotodontids might have hung on in isolation. The second factor is the pervasive influence of the small size of the skulls of the New Guinea zygomaturines which, in combination with the apparent age of the fauna, seems to have exerted a subtle bias on the interpretation of the character states of *Kolopsis rotundus*.

Stirton *et al.* (1967:151-156) observed that: "*Kolopsis rotundus* Plane 1967, represents a genus previously common in the Miocene in the middle latitudes of Australia, which lingered on into the Pliocene in the equatorial latitudes of New Guinea...", [and in relation to relict North American Tertiary faunas]..." The somewhat anomalous geochronological position of *Kolopsis rotundus*, which maintains certain primitive features [those discussed previously and dismissed as trivial] in relation to members of the subfamily occurring in somewhat older Australian faunas, indicate that a similar phenomenon has occurred in the Australian region". In light of the revised age of 2.5-3.5 million years BP for the Awe Fauna (Page and McDougal 1972, Hoch and Holm 1986), their weighting of certain characters of the P^3 of *K. rotundus* might have been different.

The heightened biochronological dissonance resulting from the revision of the age of the Otibanda Formation would seem to compel one to seek another explanation, or at least to proceed with caution. Flannery's (1988) observations seem to indicate that the relict nature of New Guinea's fauna has been fully substantiated: "By the early Miocene, geological changes had split the Australidelphian/monotreme faunas of the region into two units, a New Guinean one and and Australian one. These faunas had separate histories until the Pleistocene" (Flannery 1988:23). And "... mammalian assemblages ... from Riversleigh, Alcoota and Bullock Creek (central and northern Australia) show some striking similarities with the New Guinean mammal fauna. These assemblages include *Dorcopsis*-like macropodines ... zygomaturine diprotodontids" (Flannery 1988:18).

On the contrary; the fauna of New Guinea seems to be more representative of relatively recent adaptations to its extreme habitat diversity rather than being a refugium for archaic species. Unlike Madagascar or New Zealand, New Guinea has no radiations of disjuncts equivalent to the Malagasy lemuroids or New Zealand ratites. The unique character of the predominant large mammal elements of the New Guinea mammalian fauna (zygomaturine diprotodontids and macropodine kangaroos) appears to have originated very late in the Tertiary, probably since the mid Pliocene. However, this view does not exclude an assumption that animals had begun to colonize the presumptive New Guinea land masses since the time they had become inhabitable. The point is that the colonization of the island(s) appears to be predominantly successional over the late Tertiary as opposed to predominantly disjunct since the mid Tertiary.

CONCLUSIONS

The major conclusions drawn in this study are: 1) *Hulitherium tomasettii* and N.G. *Gen. nov.* represent species recruited from within the *Zygomaturus* clade and as such are more derived than *Zygomaturus gilli*; 2) *Kolopsis rotundus* from the late Pliocene Awe Formation of New

Guinea is more closely related to *Zygomaturus* than to *Kolopsis*; 3) *Kolopsis rotundus* appears to be most similar to the Palankarinna Lawson-Daily *Zygomaturus* sp.; 4) the stage of evolution equivalents of the Lawson-Daily Quarry *Zygomaturus* sp. or *Kolopsis rotundus* could have given rise to all later (Pleistocene) New Guinea species of the *Zygomaturus* clade (or genera of Tribe Zygomaturini) commencing in the Late Pliocene; 5) the two small Pleistocene New Guinea zygomaturines and possibly *K. rotundus* probably represent insular dwarfs; 6) the larger terrestrial fauna of New Guinea does not represent a relict Australian Miocene fauna, but does represent a mid to late Pliocene "barrel-filling" phenomenon in which a relatively few derived Australian genera have speciated prolifically and rapidly in response to availability of unoccupied niches, geographic isolation and vertically stratified habitat.

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